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ABSTRACT

The limbless caecelian amphibians have vertebral adaptations for their burrowing habit and mode of life that suggest an evolutionary change of certain thoracic vertebrae to assist motile, cervical functions, despite retention of rudimentary ribs on them. The changes appear related to distinct stresses placed on the vertebrae by movements necessary to burrowing. Also, the changes are distinct enough to be taxonomically useful for potential distinction of genera and/or species in the several families of caecelians.

INTRODUCTION

All caecilians differ from other amphibians in lacking an appendicular skeleton. Thus, without this, we lack the usual criteria for classifying the vertebrae. It is generally agreed that there is but a single cervical vertebra, the atlas, in amphibians. Yet, in caecilians the anterior four or five vertebrae function together in critical pivoting movements of the cranium. These retain free ribs, but although loss or fusion are commonly accepted as prerequisite of cervical vertebrae, that criterion is not infallible, as for example in lizards and crocodilians wherein all vertebrae anterior to the first bearing a rib articulated with the sternum are accepted as cervicals despite the fact that one or more posterior cervicals bear free ribs. A more realistic criterion for cervicals in limbless tetrapods lacking a sternum is a functional one, wherein the most anterior trunk vertebrae that serve importantly in pivotal movements of the cranium are accepted as cervicals. Therefore, in this study all of the anterior four or five trunk vertebrae are regarded as cervicals.

In the evolution of animals, changes that occur in body characteristics are the result of a cause; otherwise we would have miracles! Usually, regions having the greatest stresses (as for example the pelvic region in frogs) tend to change most extensively, to varying degree. In burrowing forms lacking limbs, the head-and-neck region evidently is just such a region of stress. For example, should an animal such as a skink find it difficult to compete with other animals for accustomed food, it either becomes extinct or acquires an ability to augment the food supply from another source. A source often sought by such types of animals, is within a few inches of the accustomed habitat, but involves burrowing in the earth, where insects, insect larvae, worms, etc. are usually available. Animals adapting for exploitation of such food resources find limbs and digits actually a hindrance, particularly if the adaptation leads to the use of burrows for permanent habitat. Thus, in a number of cases, we find the digits are discarded one by one and finally the entire limb may be lost.

Animals having run the full gamut of such burrowing adaptation, with complete loss of limbs, of necessity will be forced to use the head or neck for burrowing if it continues its course of adaptation to that way of life. Perhaps at this point, most snake phylogenies parted company with other invaders of the burrowing adaptive zone, failing to evolve the subsequently essential perfections that more successful burrowers, such as the Scolecophidia, caecilians and amphisbaenids, have devised.

The present study is an attempt to determine whether support for this hypothesis may be evident in modifications, if any, that may have taken place in the anterior vertebrae of caecilians.

Unfortunately, a limited number of species has been available for examination. Thus, the number of samples I have used is far too small to justify generalizations about consistency of structure in orders or families or perhaps even in genera. However, one may reasonably presume that the differences pointed out are obvious from the illustrations and would be evident in other examples of comparable size and age.

I am not alone in considering generic and specific differences to exist in the contours of vertebrae. Recently, a single, small, broken vertebra found in Brasil served as the type for a new species and genus of fossil caecilians and led the describers to postulate a closer relationship with an African genus than with other American genera.

Such photographs as I have were prepared several years ago; but I was unable to obtain as much material for making skeletons as I desired and I withheld publication until now, hoping to acquire a more adequate representation of species.

ACKNOWLEDGMENTS

The following abbreviations are used: AMNH—American Museum of Natural History, New York, New York; ANSP—Academy of Natural Sciences, Philadelphia, Pennsylvania; DSBM—Division of Systematic Biology, Stanford University, California; EHT-HMS—Edward Taylor-Hobart M. Smith, Lawrence, Kansas; MCZ—Museum of Comparative Zoology, Harvard University; UIM—University of Illinois Museum of Natural History, Urbana, Illinois.

DESCRIPTIONS OF CERVICAL VERTEBRAE

FAMILY SCOLECOMORPHIDAE

Scolecomorphus kirkii Boulenger (Fig. 1). Upper portion of the first (atlas) vertebra very much longer than the ventral portion. No dorsal ridges evident on the vertebrae; ridges on ventral surfaces strongly marked, widening posteriorly, closely held by the anterior processes which are curved slightly inwardly.

FAMILY TYPHLONECTIDAE

Typhlonectes natans (Fischer in Peters) (Fig. 2). Total length of atlas much greater than median ventral length. Dorsal

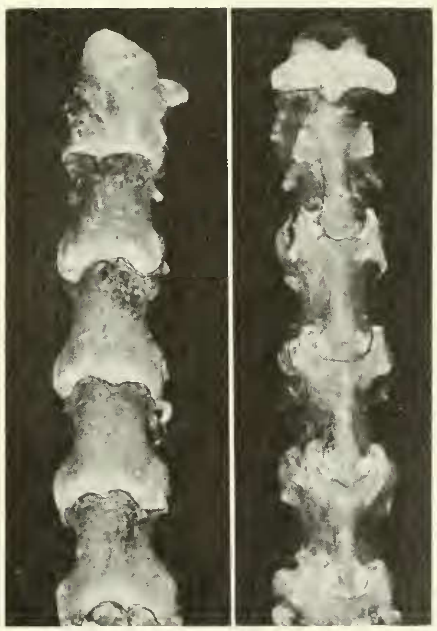


FIG. 1. *Scolecomorphus kirkii* Boulenger. MCZ 27106, Cholo Mountains, Malawi, Africa, "elev. 3600 ft." (see Table 4, U. Kan. Sci. Bull., vol. 48, p. 602). A, Dorsal view of 5 cervical vertebrae. B, Ventral view of same.

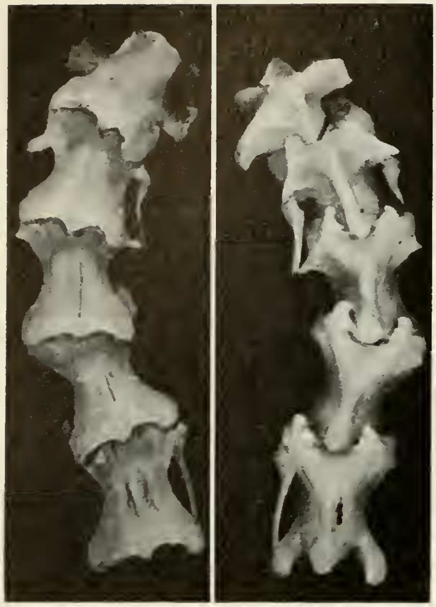


FIG. 2. *Typhlonectes natans* (Fischer in Peters). MCZ 24524, Río Magdalena, Cucutá, Colombia, South America. A, Dorsal view of 5 cervical vertebrae. B, Ventral view of same.

ridges not or scarcely indicated, but the third and fourth vertebrae each with weak, paramedian dorsal grooves, the fifth vertebra with two stronger parallel dorsal grooves. On the ventral surface the ventral ridge is somewhat curving or saddle-shaped. The fifth has a deep groove on each side of the ventral ridge. Ribs still remain on the second and fifth vertebrae. The anterior processes of the ventral part of each vertebra are moderately close to the preceding vertebra, and tend to curve in slightly.

FAMILY ICHTHYOPHIIDAE

Ichthyophis kohtaoensis Taylor (Fig. 3A, B; Fig. 4B, C). In Fig. 3, length of dorsal part of atlas 27 mm; length of ventral portion of axis 15 mm. Dorsal ridges very strong on second to fifth vertebrae; anterior processes of third vertebra grasping the ventral ridge of the preceding vertebra, those on the following two vertebrae curving inward around the posteriorly widened part of the ventral ridge of preceding vertebrae.

In Fig. 4, in ventral view, the processes directed forward on vertebrae four and five widely separated. A ventral ridge barely indicated on the fourth vertebra. In dorsal view, only a vague suggestion of a dorsal ridge. Four have ribs attached.

Ichthyophis beddomei Peters (Fig. 3C, D). Length of dorsal part of atlas much longer than ventral portion. The paired ventral processes extending forward from the third to the fifth vertebrae are nearly parallel, rather than curving inward. No dorsal ridges; strong ventral ridges, their posterior terminal portions widened. Two ribs attached.

Ichthyophis mindanaoensis Taylor (Fig. 4A). A dorsal view of four vertebrae, the posterior three with a very low dorsal ridge.

Caudacaecilia larutensis Taylor (Fig. 5A, B). Dorsal length of axis only a little longer than ventral length. A vague suggestion of dorsal ridges on vertebrae; well-defined ventral ridges widening posteriorly. Processes on rib attachment somewhat elongated anteriorly.

Caudacaecilia nigroflava Taylor (Fig. 5C, D). Dorsal length of axis only two or three mm greater than ventral length. Anteriorly directed ventral processes parallel.

FAMILY CAECILIIDAE

Oscaecilia bassleri (Dunn) (Fig. 6A, B). On five anterior vertebrae, the dorsal ridge is only vaguely indicated. Ventral ridge on vertebrae 2 and 4 relatively very narrow throughout most of its length, widening suddenly posteriorly. A pair of small projections from the forwardly directed processes seemingly serve as braces. They are directed inwardly and somewhat backward.

Oscaecilia ochrocephala (Cope) (Fig. 6C, D). Five anterior vertebrae with well-defined dorsal ridges. In ventral view, the

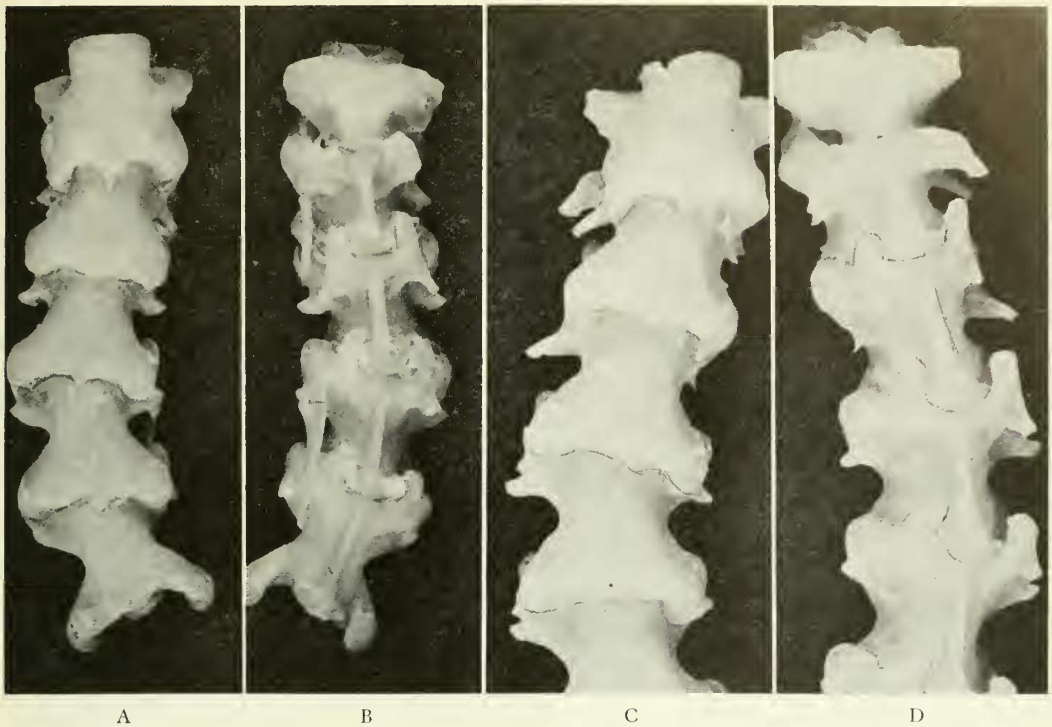


Fig. 3. A-B, *Ichthyophis kohtaoensis* Taylor. EHT-HMS 3935, 10 miles N Chiang Dao, northern Thailand. A, Dorsal view of 5 cervical vertebrae. B, Ventral view of same. C-D, *Ichthyophis beddomei* Peters. EHT-HMS 3186, Kotegehar, India. C, Dorsal view of 4 cervical vertebrae. D, Ventral view of same.

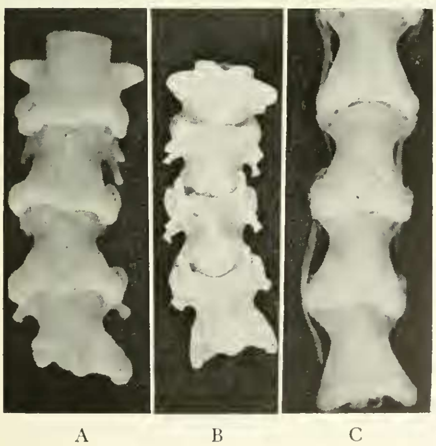


Fig. 4. A, *Ichthyophis mindanaoensis* Taylor. DSBM 20926, 11 km SE Buena Suerte, on side of Dapitán Peak, Mindanao, "elev. 3700 ft." Dorsal view of cervical vertebrae. B, *Ichthyophis kohtaoensis* Taylor. EHT-HMS 1838, Dansai Province, Thailand. Four cervical vertebrae, ventral view. C, *Ichthyophis kohtaoensis* Taylor. DSBM 25496, Kerala Forest, India. Body vertebrae, from near middle of body, dorsal view.

processes enclosing the preceding vertebra much thickened, slightly curving in. The ventral ridge sharply defined and strongly widened posteriorly, somewhat pointed terminally. The differences between the dorsal and ventral views of these two presumed species of the same genus is remarkably great.

Caecilia albiventris Daudin (Fig. 7A, B). Five anterior vertebrae, all except atlas with a well-defined narrow dorsal ridge. A well-defined ventral ridge on all but axis, all widening posteriorly. The vertebrae of *albiventris* are relatively narrower than most vertebrae of *Caecilia*. The forwardly-directed ventral processes are nearly parallel and lack small, inwardly-directed processes.

Caecilia degenerata Dunn (Fig. 7C, D). Four anterior vertebrae, the second and third each with a vague, dorsal ridge

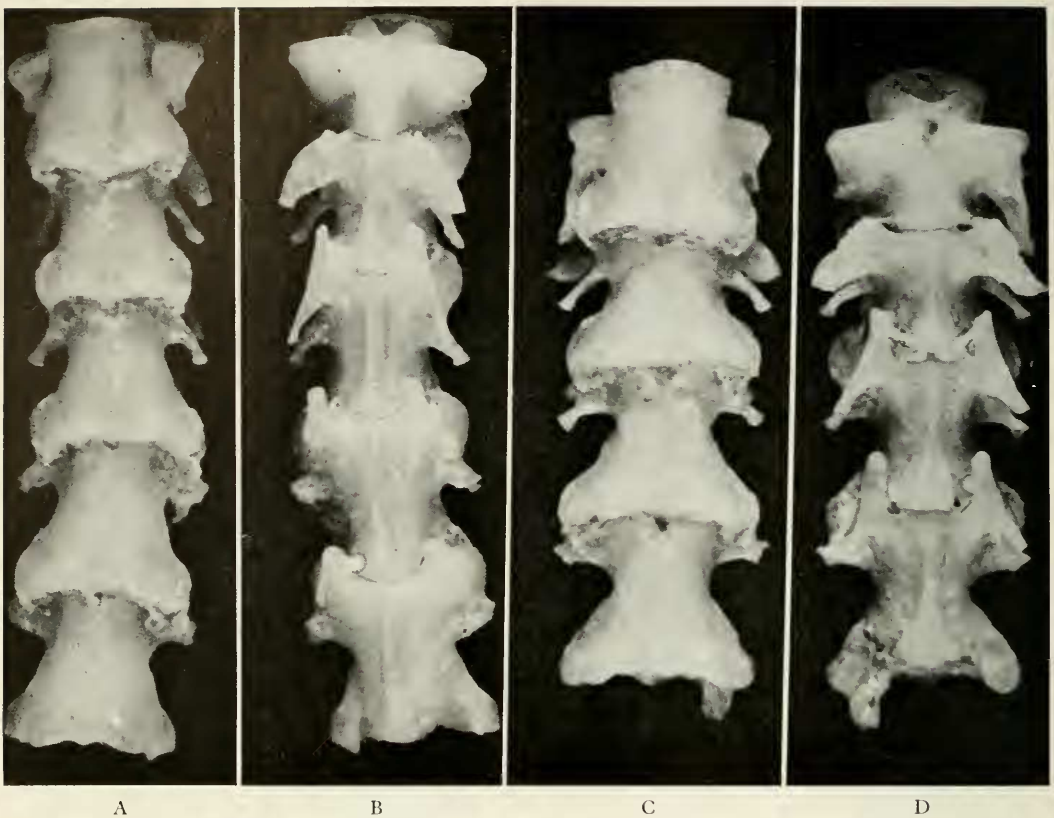


FIG. 5. A-B, *Caudacaecilia larutensis* (Taylor). EHT-HMS 3359, Maxwell Hill, Larut Hills, Perak, Malaya (topotype, within ½ mile of type-locality). A, Dorsal view of 4 cervical vertebrae. B, Ventral view of same. C-D, *Caudacaecilia nigroflava* (Taylor). EHT-HMS 8375, Bukit Lagong Forest Reserve, Selangor, Malaya. C, Dorsal view of 5 cervical vertebrae. D, Ventral view of same.

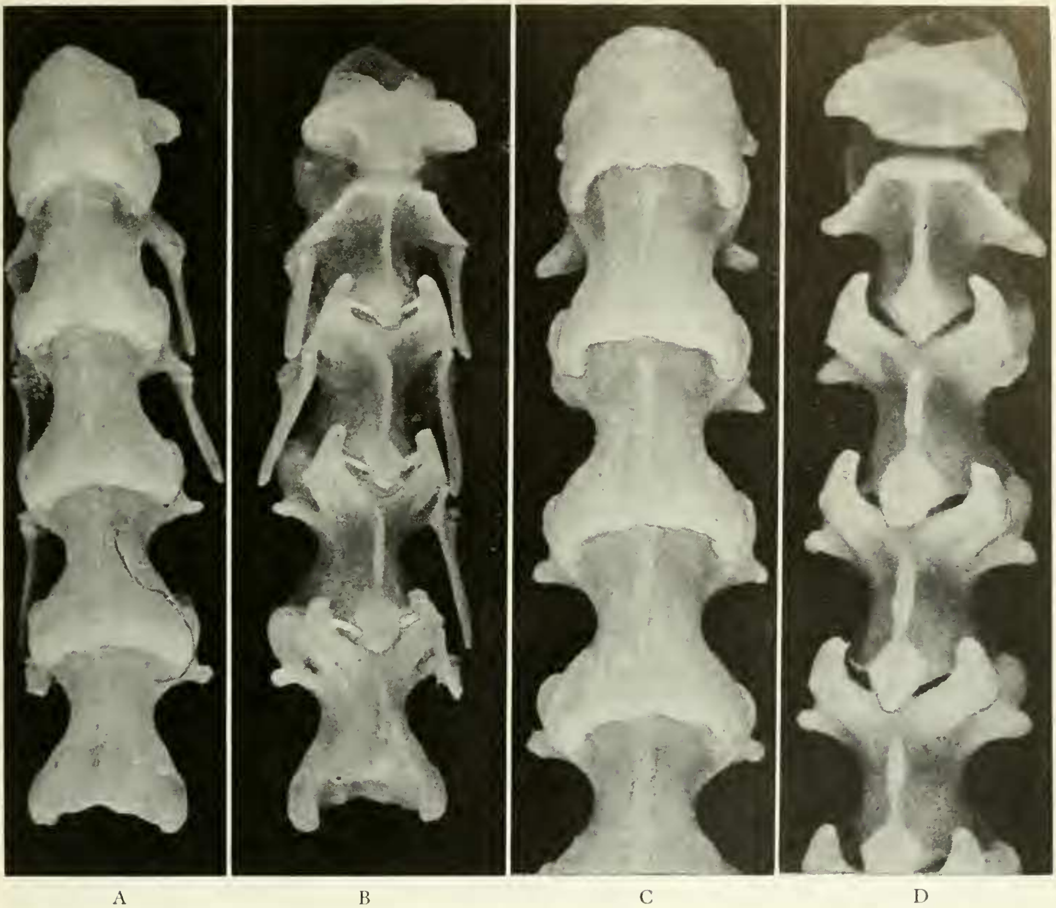
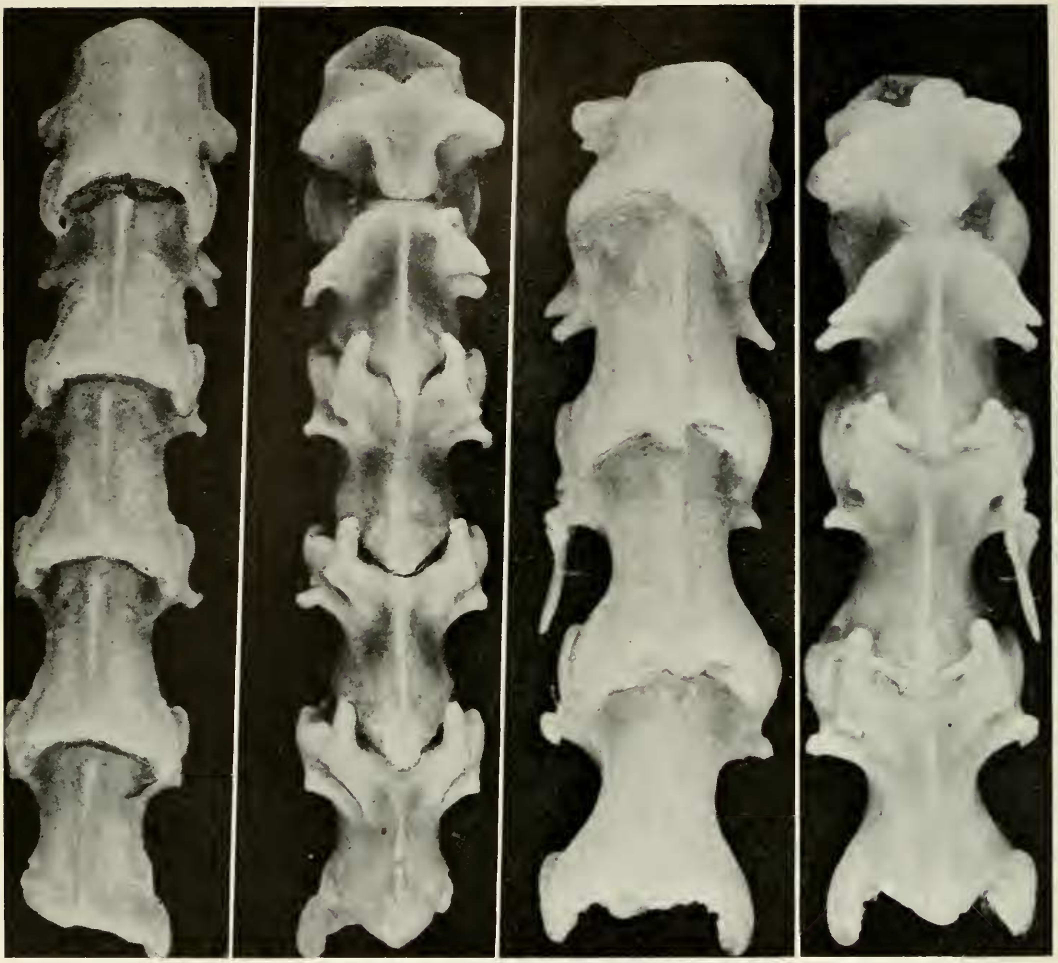


FIG. 6. A-B, *Oscaecilia bassleri* (Dunn). EHT-HMS 4675, "Ecuador." A, Five cervical vertebrae, dorsal view. B, Ventral view of same. C-D, *Oscaecilia ochrocephala* (Cope). UIM 41092, Gatún, Canal Zone, Panamá. C, Five cervical vertebrae, dorsal view. D, Ventral view of same.



A B C D

Fig. 7. A-B, *Caecilia albiventris* Daudin. AMNH 49960, "Bogotá" Colombia, S.A. A, Cervical vertebrae, dorsal view. B, Ventral view of same. C-D, *Caecilia degenerata* Dunn. AMNH 23354, "Colombia, S.A." C, Cervical vertebrae, dorsal view. D, Ventral view of same.

extending to posterior border of the vertebra. In ventral view, with very narrow, clearly-defined ridges widening slightly posteriorly. The forward processes of third and fourth each with a small branch pointing inward and somewhat backward.

Caecilia occidentalis Taylor (Fig. 8A, B). Four anterior vertebrae relatively broad, with slight median ridges on last three. In ventral view, the last three with low ridges; forwardly-projecting processes widely separated, nearly parallel.

Caecilia disossea Taylor (Fig. 8C). Ventral view of the first five vertebrae with last four showing a narrow, sharply-defined ventral ridge that curves down and widens a little posteriorly. The ventral processes directed forward, rounded at tips, not parallel, lacking any internal directed branches.

Caecilia orientalis Taylor (Fig. 8D). A vague, dorsal ridge indicated on posterior three of the four anterior vertebrae. In ventral view, with three, sharply-defined ventral ridges tending to narrow mesially and widen slightly at posterior end. Proc-

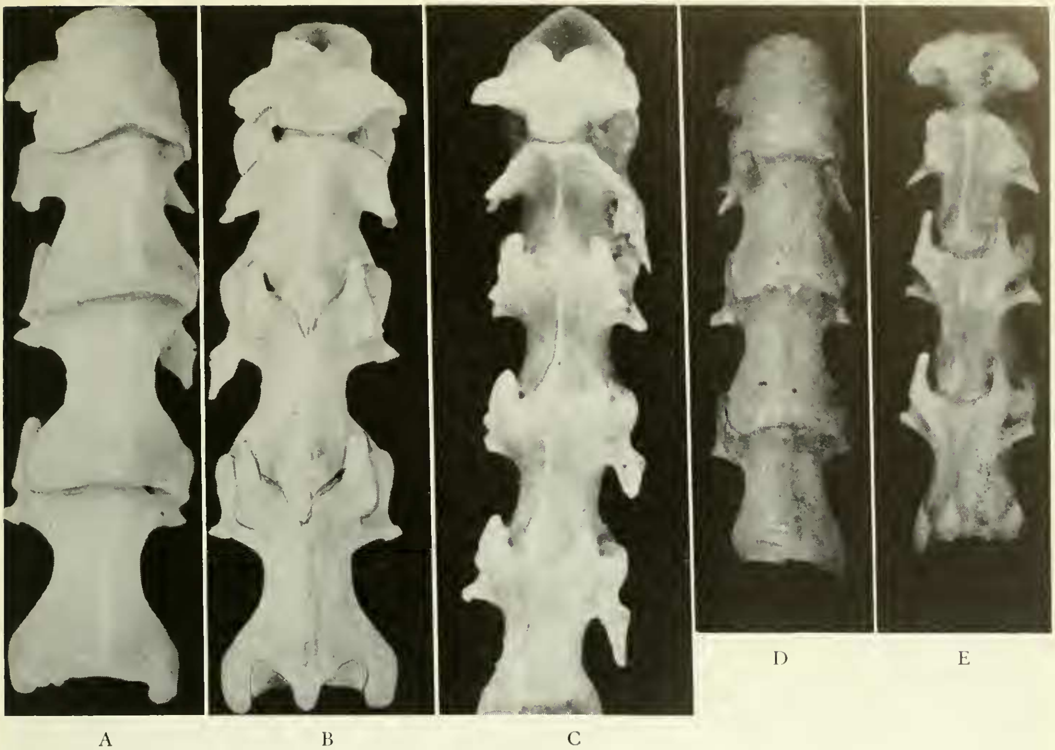


Fig. 8. A-B, *Caecilia occidentalis* Taylor. ANSP 25568, Popayán, Cauca, Colombia, S.A. A, Cervical vertebrae, dorsal view. B, Ventral view of same. C, *Caecilia disossea* Taylor. EHT-HMS 1808, Alto Curaray, Napo Pastaza, Ecuador, S.A. Four cervical vertebrae, ventral view. D-E, *Caecilia orientalis* Taylor. EHT-HMS 4677, "Ecuador," S.A. D, Four cervical vertebrae, dorsal view. E, Ventral view of same.

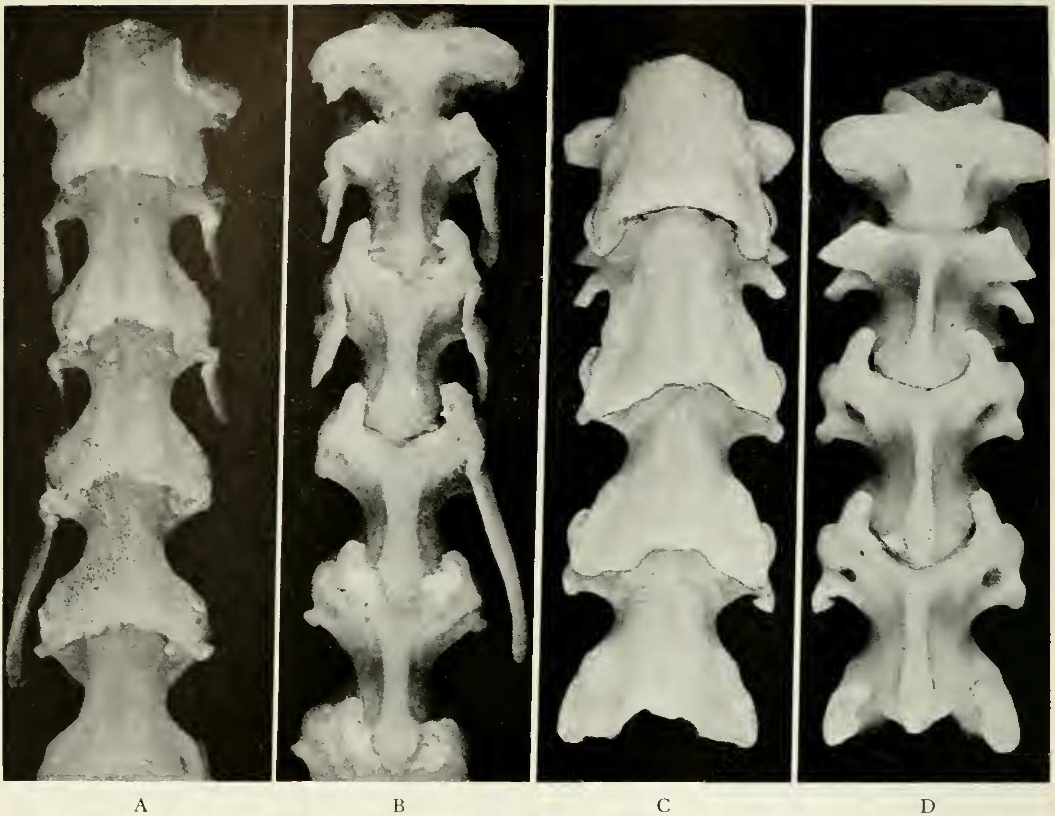


FIG. 9. A-B, *Gymnopis multiplicata* Peters. EHT-HMS 4702, Rancho San Bosco, Tilarán, Guanacaste Province, Costa Rica. A, Five cervical vertebrae, dorsal view. B, Ventral view of same. C-D, *Dermophis mexicanus* Duméril and Bibron. UIM 66889, Chiapas, Mexico. C, Four cervical vertebrae, dorsal view. D, Ventral view of same.

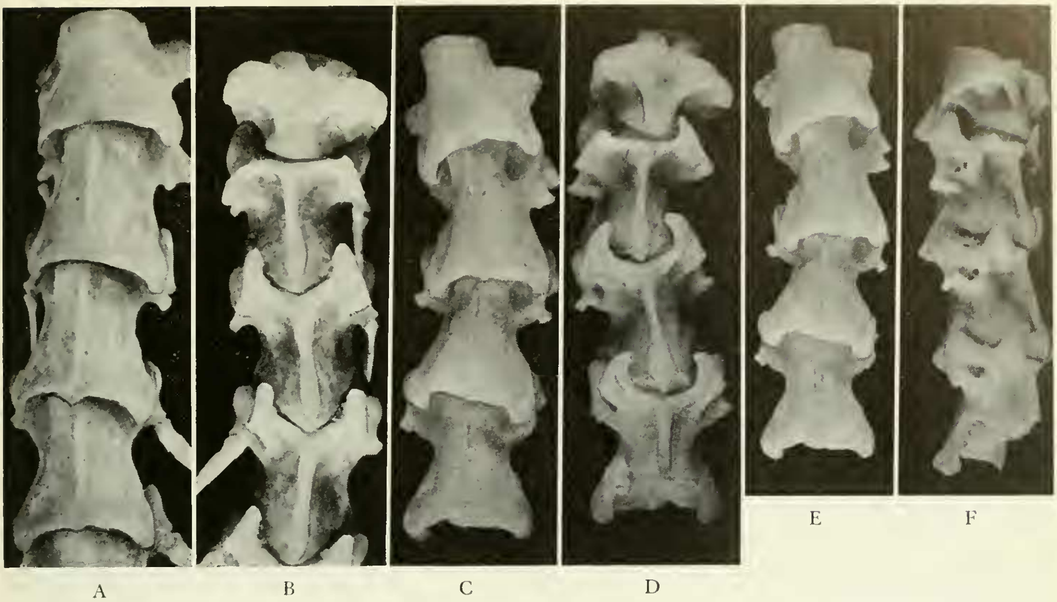


FIG. 10. A-B, *Siphonops paulensis* Boettger. AMNH 23433, "Brasil." A, Four cervical vertebrae, dorsal view. B, Ventral view of same. C-F, *Siphonops annulatus* (Mikan). UIM 56668, Limón Cocha, Ecuador, S.A. C, Four cervical vertebrae, dorsal view. D, Ventral view of the same. E, Four cervical vertebrae, dorsal view. F, Lateral view of same.

esses relatively slender, nearly parallel and rather widely separated.

Gymnopis multiplicata Peters (Fig. 9A, B). Five anterior vertebrae, in dorsal view with practically no traces of ridges. In ventral view, with a relatively broad ventral ridge, a widening posteriorly, the forward-directed processes heavy, somewhat blunted at their tips, not exactly parallel. The third has a pair of small branches from the forward projecting processes.

Dermophis mexicanus Duméril and Bibron (Fig. 9C, D). Four anterior vertebrae showing dimly a median ridge on last three. The lower lateral parts of the vertebrae show a more or less distinct elevation. In ventral view, the last three with sharply defined ventral ridges widening but slightly posteriorly. Forwardly directed processes curving inwardly somewhat.

Siphonops paulensis Boettger (Fig. 10A, B). Four anterior vertebrae, with distinct ridges the greater part of dorsal length. Sharply defined ventral ridges widening very slightly posteriorly; processes at terminal forward part, parallel.

Siphonops annulatus (Mikan) (Fig. 10C, D). Four anterior dorsal vertebrae with a very narrow dorsal ridge scarcely discernible. In ventral view, strong but rather narrow median ridge, widening posteriorly somewhat, the processes directed forward and curving inwardly as if grasping. In lateral view, foramina for blood vessels and nerves evident.

Geotrypetes seraphini seraphini (A. Duméril) (Fig. 11A, B). Atlas smaller than usual. The third and fourth anterior dorsal vertebrae are elongated more than in most forms. In ventral view, anterior border of second vertebra circular rather than angular. Third and fourth vertebrae elongate, the processes nearly parallel, the ventral ridge prominent for most of length. Median ventral length of axis very short.

Schistometopum gregorii (Boulenger) (Fig. 11C, D). Four anterior vertebrae, the last three with a low dorsal ridge. In ventral view, the lower part of the atlas longer than in *G. seraphini*. The frontal

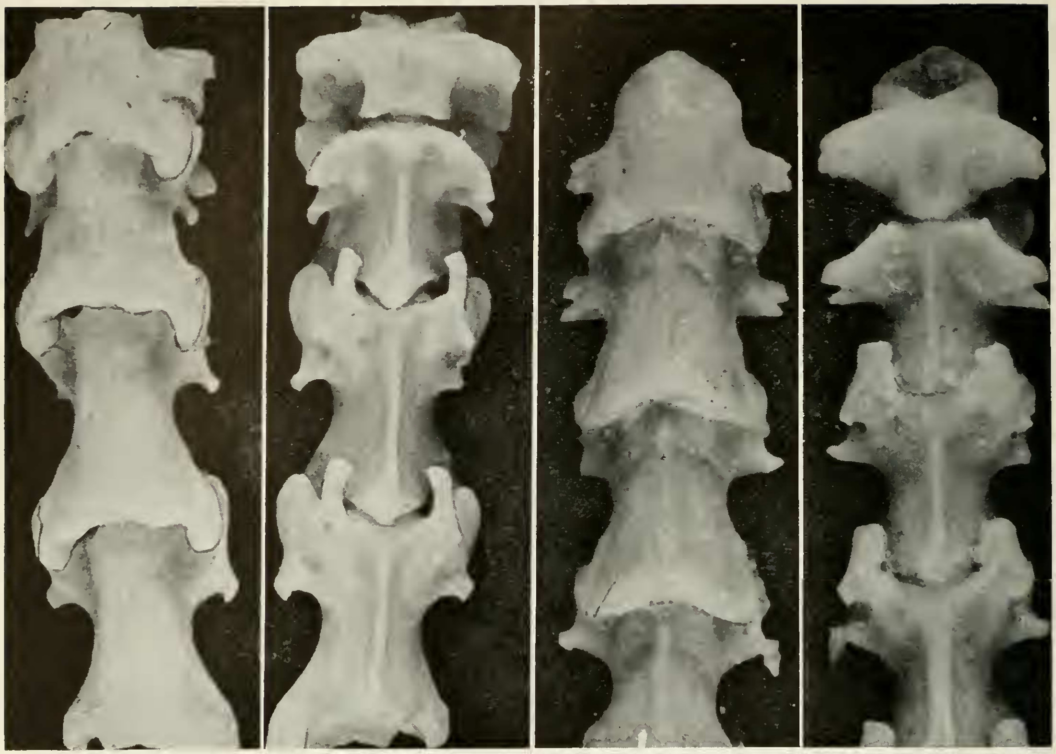


FIG. 11. A-B, *Geotrypetes s. seraphini* (A. Duméril). MCZ 3424, Metet, Cameroons, Africa. A, Four cervical vertebrae, dorsal view. B, Ventral view of same. C-D, *Schistometopum gregorii* (Boulenger), MCZ 20146, Lake Peccatoni, Kenya, Africa. C, Four cervical vertebrae, dorsal view. D, Ventral view of same.

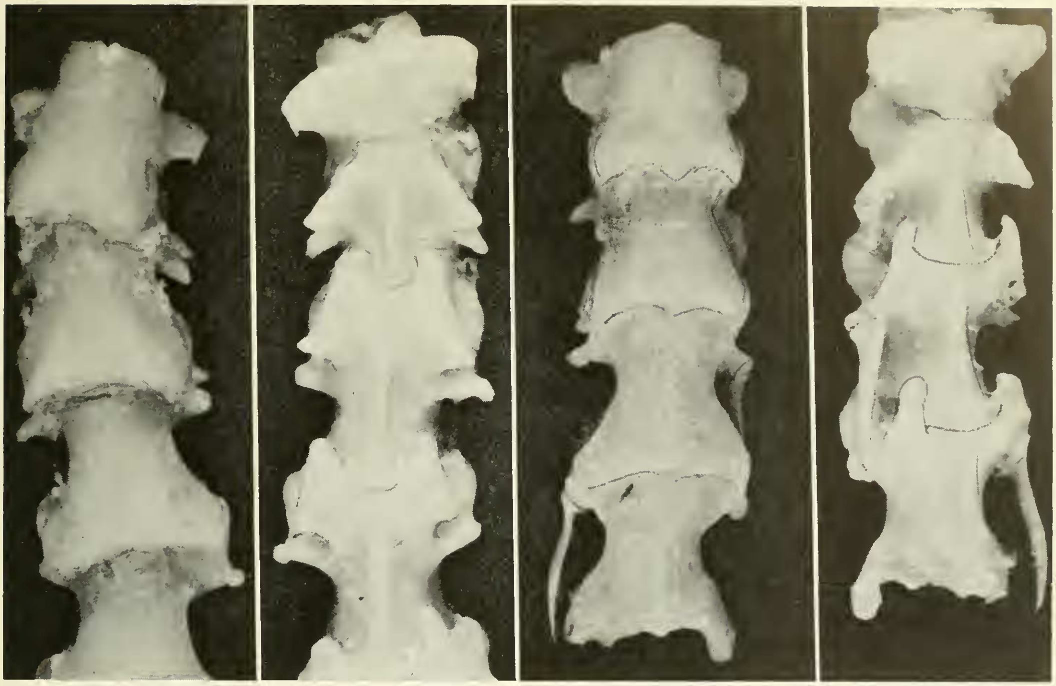
border of the second ventral is strictly angular. The forward-directed processes are much thickened, nearly parallel and not terminally rounded; well-developed ventral ridges.

Hypogeophis r. rostratus (Cuvier) (Fig. 12A, B). Four anterior vertebrae, without trace of dorsal ridges. In ventral view, each with a median ridge, at least on last half of ventral surface, widening posteriorly. The second is angular anteriorly, the posterior part of ridge closely bordered by nearly parallel forward projections; following vertebrae with processes longer and merging, extending outward somewhat.

Uraeotyphlus oxyurus Duméril and Bibron (Fig. 12C, D). Four anterior vertebrae, the posterior ones with a vague dorsal ridge. In ventral view, with a thin, slightly developed ventral ridge, widening posteriorly, and curving down slightly posteriorly. Forward-directed processes widely separated, nearly parallel anteriorly.

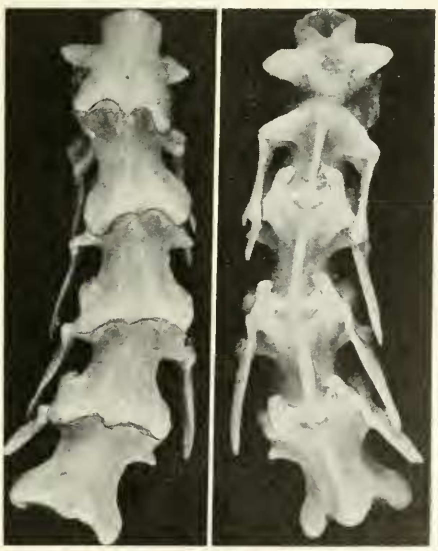
Grandisonia alternans Stejneger (Fig. 13). Five anterior vertebrae, not or only vaguely suggesting dorsal ridges on four posterior ones. Most ribs retained. In ventral view, each with a strongly-defined ventral ridge becoming widened at the posterior terminal, almost as if formed by two branches. Forward processes tending to curve inwardly.

Gegeneophis ramaswamii Taylor (Fig. 14A, B). Four anterior vertebrae, the third and fourth showing vague dorsal ridges. In ventral view, posterior vertebrae with moderately well-defined ventral ridges, the



A B C D

Fig. 12. A-B, *Hypogeophis r. rostratus* (Cuvier). MCZ 48935, St. Anne Island, Mahe Coast, Seychelles Islands. A, Cervical vertebrae, dorsal view. B, Ventral view of same. C-D, *Uraeotyphlus oxyurus* Duméril and Bibron. MCZ 9484, Taliparabambia, Travancore, India. C, Four cervical vertebrae, dorsal view. D, Ventral view of same.



A B

Fig. 13. *Grandisonia alternans* Stejneger. EHT-HMS 4647 (formerly MCZ 15638), Mahe, Seychelles Islands. A, Five cervical vertebrae, dorsal view. B, Ventral view of same.

A B

Fig. 14. *Gegeneophis ramaswamii* Taylor. EHT-HMS no no., no locality. A, Four cervical vertebrae, dorsal view. B, Ventral view of same.

terminal part of forward processes nearly parallel.